Relationships Between Geodiversity and Vegetation in South-eastern Australia

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Geodiversity, the natural range of geological, geomorphological and soil features, is thought to play a key role in the development of Australian ecosystems and evolution of their biota, due to the widespread occurrence of old soils with impoverished nutritional status and the comparatively restricted occurrence of fertile soils. While associations between soils and vegetation characteristics such as scleromorphy were first noted a century ago, modern theories propose evolutionary and ecological processes that shaped Australian flora and vegetation through interactions between soil nutrition, plant functional traits and flammability. Evidence in support of these generalisations comes mainly from site-specific empirical studies, surveys of plant traits and their associations, classification and mapping of land systems, analyses of regional environmental gradients and phylogenetic studies. The extent to which soils and the substrates from which they are derived place constraints on the climatic response of biota has important implications for understanding future responses of the biota to anthropogenic climate change. Yet, worldwide, there are few studies that examine the relative contributions of geological substrates and climate to variation in vegetation properties over extensive sub-continental regions. This study used a spatially explicit approach to examine the relationship between vegetation and geological substrates over New South Wales, a region of 80 million hectares in south-eastern Australia spanning a diverse range of geology, vegetation and climate. It aimed to assess the fidelity of major vegetation types to geological substrates and estimate the overall influence of geodiversity on vegetation composition relative to that attributable to climate. The spatial data were drawn from maps produced by geological and vegetation surveys. Geological maps were re-classified into 16 broad units reflecting textural and mineral characteristics considered likely to be influential on plant growth. They represent a component of total geodiversity related to broad landscape-scale patterns in major bedrock and regolith types. Vegetation maps were re-classified in 16 broad formations reflecting structural, physiognomic and functional characteristics of vegetation, and into a larger number of 99 classes reflecting species composition. The two spatial data sets were analysed to determine the diversity of vegetation types within geological units and fidelity of each vegetation type to each geological unit. The relative influence of climatic co-variables was also examined using spatial surfaces spline-fitted to 30 years of weather station data. The results indicate a strong non-random relationship between vegetation and geodiversity, with most vegetation types restricted to a narrow range of geological substrates. Partial variance analyses indicated that the influence of geodiversity on vegetation composition was stronger than, and largely independent of the influence of climate. Consistent with current theories, sclerophyllous vegetation formations and classes showed a strong association with geological units characterised by low levels of mineral nutrients. It was concluded that landscape patterns of geodiversity are likely to place significant constraints on the response of native vegetation to future climate change.

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INTRODUCTION

Geodiversity is the natural range (diversity) of geological (rocks, minerals, fossils), geomorphological (land form, processes) and soil features. It includes their assemblages, relationships, properties, interpretations and systems (Gray 2004). Many of the earliest phytosociological studies in south-eastern Australia noted the association between plants and the geological substrates and land forms on which they grow (McLuckie & Petrie 1927, Pidgeon 1937, Fraser & Vickery 1939, Crocker 1944, Beadle 1948). The soils produced by weathering of these substrates in particular geomorphic settings vary greatly in levels and proportions of mineral nutrients, and in their textural and structural characteristics that govern their capacity to retain moisture and conduct subterranean oxygen. Different plant species vary in their ability to extract these three essential resources and to tolerate extreme levels of supply. Species that share similar ranges of tolerance to soil-related resources may therefore be expected to co-occur within communities on particular groups of geological substrates, at least in cases where there is vertical concurrence between soils and the underlying substrate.

At biogeographic scales, geological substrates are thought to play a key role in the development of Australian ecosystems and evolution of their biota, due to the widespread occurrence of old soils with impoverished levels of nutrients and the comparatively restricted occurrence of fertile soils. Diels (1906) first noted a distinction between sclerophyll vegetation associated with sandy soils and 'savanna' vegetation associated with 'favourable' soil conditions. Andrews (1916) later proposed a connection between sclerophylly (a syndrome typified by small, thick leaves with thick cuticles and abundant sclerotic tissue) and soil nutrition, particularly nitrogen and calcium. By mid-century, empirical evidence was emerging that physiological and morphological traits related to uptake of phosphorus (Beadle 1953), acquisition of nitrogen (Hannon 1956) and accumulation of aluminium (Webb 1954) were closely associated with acidic, nutrient-deficient soils that occur in certain parts of the Australian continent. Modern theories propose evolutionary and ecological processes that shaped Australian flora and vegetation through interactions between soil nutrition, plant functional traits and flammability (Beadle 1966, Orions & Milewski 2007, Hopper 2009, Lambers et al. 2010). Evidence in support of these generalisations comes mainly from empirical site-specific or autecological studies (Beadle 1954, Webb 1954, Lamont 1982, Shane & Lambers 2005), surveys of plant traits and their associations (Gill 1975, Lambers et al. 2010), the classification and mapping of land systems – areas of recurring patterns in topography, soils and vegetation (Christian 1952), analyses of local and regional environmental gradients (Myerscough & Carolin 1986, Keith & Sanders 1990) and phylogenetic studies (Johnson & Briggs 1975, Crisp et al. 2004).

Sclerophyll elements of Australian vegetation appear to have originated on pockets of oligotrophic soils in the Cretaceous (Hill et al. 1999, Crisp et al. 2004), yet they did not diversify and rise to dominance until 25 – 10 million years ago. Their expansion and diversification was at the expense of mesic forest vegetation, and coincided with climatic cooling, drying and increased seasonality as separation of Australia and South America from Antarctica initiated circum-polar oceanic currents (Crisp et al. 2004). Expansion and diversification of the Australian arid flora occurred more recently, 5 – 2 million years ago, as the continent moved still further north and experienced extreme wet-dry glacial cycles (Crisp et al. 2004). Fires also became prominent periodically and influential on vegetation during this period (Keeley & Rundel 2005). Yet strong edaphic patterns apparently persisted through this history and remain in the contemporary vegetation (Hopper 2009) and, despite major extinctions and radiations associated with climatic upheavals, there is evidence of biome conservatism in a large majority of lineages (Crisp et al. 2009).

While both soils and climate play prominent roles in theories of the evolutionary history of species within Australian vegetation (Crisp et al. 2004, Orians & Milewski 2007, Hopper 2009), their historical inter-relationships are poorly understood. How much did soils constrain the historical responses of vegetation to climate change? This question seems crucial to understanding the future response of biota as anthropogenic climate change unfolds, yet the spatial dimensions of historical biomes are difficult to quantify and hitherto remain largely unexplored. Insights can possibly be gained by using spatially explicit data to study contemporary relationships between vegetation, soils and climate, yet this has not been examined at the level of assemblages over extensive bioregional scales.

This study investigated the relative influence of geological substrates and climate on the biogeography of vegetation at a sub-continental spatial scale. Its aims were: i) to determine the fidelity between major vegetation types and geological substrates; and ii) to estimate the relative contribution of substrates and climatic variables to variation in species composition of the vegetation. The study was carried out across

New South Wales, a region of 80 million hectares in south-eastern Australia that currently encompasses a diverse range of vegetation, geology and climate. Historically, the region underwent profound climatic upheaval since the appearance of flowering plants in the Cretaceous. A spatially explicit approach was applied using map data synthesised from extensive vegetation and geological surveys carried out within the region (Keith 2004, Stewart et al. 2006). The two spatial data sets were first analysed to assess the fidelity between vegetation types and geological units. A second analysis was carried out to assess the relative influences of geological substrate and climatic factors on the species composition of vegetation. Both analyses were carried out on broad scale classifications reflecting on respective maps the broad structural, physiognomic and functional characteristics of vegetation and the broad textural and mineral characteristics of geological substrates.

METHODS

Vegetation map

The vegetation map was assembled from 105 source maps covering various subregions within New South Wales. These source maps employed a range of different vegetation classifications, varying spatial scales and overlapped with one another spatially to varying degrees. To simplify and standardise the source maps to a common format, the legend of each was re-classified into the vegetation formations and classes described by Keith (2004). In this classification 16 broad formations and sub-formations represent variation in structural, physiognomic and functional characteristics of vegetation (Table 1), and 99 vegetation classes nested within them represent variation in vascular plant species composition (Keith 2004). Classes are not strictly nested within formations, as structure may vary considerably within compositionally defined units, however, classes were assigned to the vegetation formation representing the most commonly expressed structural, physiognomic and functional features of a mature stand (Keith 2004).

The 105 source vegetation maps were ranked according to their relative reliability based on assessments of classification skill, thematic and spatial resolution and currency using a protocol adapted from the one described by Keith & Simpson (2006). After standardising their spatial projections to the Australian Geodetic Datum 66 and Lamberts Conformal projection in a geographic information system, the source maps were merged sequentially so that features of the most reliable source map were displayed in preference to those of other maps wherever there were spatial overlaps (Keith 2004). A similar procedure was used to prepare a mask of extant native vegetation by reclassifying each legend category of each source map as native or non-native and then merging according to the currency of remote imagery from which each source map was derived. The mask was then applied to the composite map to derive an updated version (v3.0) of the vegetation map of NSW and the ACT prepared earlier by Keith (2004) (Fig. 1).

Geological substrate map

A map of geological substrates was derived from spatial data on the surface geology of Australia (Stewart et al. 2006) which, for New South Wales, was based primarily on mapping prepared by the Geological Survey of New South Wales (GSNSW, http://www.dpi.nsw.gov.au/minerals/geological/geological-maps). This dataset shows the distribution of 785 geological units (mainly at Geological Formation level) and was generalised largely from the state digital geology dataset as at 2003, comprising the GSNSW 1:100 000 and 1:250 000 geological map series. Some areas in the north-east of the state (eg: Moree, Inverell, Tamworth, Manilla) and central-west (eg: Goulburn, Lake Cargellico) were re-compiled from more recent data sourced from GSNSW in 2004-5 (Stewart et al. 2006). The basement geology of the Broken Hill region was compiled from 1996 1:500 000 scale data from the national, NSW and South Australian geological surveys. Mapping for the Murray Basin region was compiled from 1991 1:1 000 000 scale data from the Australian Geological Survey Organisation (AGSO). To compile a seamless state dataset, the original map data were edited along the edges of source datasets (edge-matching), which varied in age and spatial scale of compilation. Adjustments to some older geological data were made using geophysical data interpretation where particularly poor edge-matching or spatial accuracy (± 1 km) was identified in the source data (Stewart et al. 2006).

The spatial data prepared by Stewart et al. (2006) generally did not distinguish contrasting depositional environments of unconsolidated Quarternary sediments along the coast. To resolve this deficiency, the coastal portion of Stewart's map was overlain by more recent 1:25 000 scale mapping of coastal Quarternary geology, which discriminated a further 48 units of sediments with alluvial, estuarine and coastal barrier depositional systems (Troedson & Hashimoto

Table 1. Vegetation formations of New South Wales.

Formation	Description
Rainforests	Forests of broad-leaved mesomorphic trees, with vines, ferns and palms. Includes Cunoniaceae, Sapindaceae, Monimiaceae, Lauraceae, Meliaceae, Myrtaceae, Apocynaceae, Rubiaceae, Aspleniaceae, Dryopteridaceae. Coast and tablelands in mesic sites on fertile soils.
Wet sclerophyll forests (shrubby subformation)	Tall forests of scleromorphic trees (typically eucalypts) with dense understories of mesomorphic shrubs, ferns and forbs. Includes Myrtaceae, Rubiaceae, Cunoniaceae, Dryopteridaceae, Blechnaceae, Asteraceae. Relatively fertile soils in high rainfall parts of coast and tablelands.
Wet sclerophyll forests (grassy subformation)	Tall forests of scleromorphic trees (typically eucalypts), with grassy understories and sparse strata of mesomorphic shrubs. Includes Myrtaceae, Poaceae, Euphorbiaceae, Fabaceae, Casuarinaceae and Asteraceae. Coast and tablelands in high rainfall regions on relatively fertile soils.
Grassy woodlands	Woodlands of scleromorphic trees (typically eucalypts), with understories of grasses and forbs and sparse shrubs. Includes Myrtaceae, Poaceae, Asteraceae, Epacridaceae and Pittosporaceae. Rolling terrain with fertile soils and moderate rainfall on the coast, tablelands and western slopes.
Grasslands	Closed tussock grasslands with a variable compliment of forbs. Includes Poaceae, Asteraceae, Fabaceae, Geraniaceae and Chenopodiaceae. Fertile soils of the maritime zone, tablelands and western floodplains.
Dry sclerophyll forests (shrub/grass subformation)	Forests of scleromorphic trees (typically eucalypts), with mixed semi-scleromorphic shrub and grass understories. Includes Myrtaceae, Poaceae, Asteraceae, Ericaceae, Dilleniaceae and Fabaceae. Moderately fertile soils in moderate rainfall areas of the coast, tablelands and western slopes.
Dry sclerophyll forests (shrubby subformation)	Low forests and woodlands of scleromorphic trees (typically eucalypts), with understories of scleromorphic shrubs and sparse groundcover. Includes Myrtaceae, Proteaceae, Ericaceae, Fabaceae and Cyperaceae. Regions receiving high to moderate rainfall on the coast, tablelands and western slopes.
Heathlands	Dense to open shrublands of small-leaved scleromorphic shrubs and sedges. Includes Proteaceae, Fabaceae, Myrtaceae, Casuarinaceae and Cyperaceae. High rainfall regions of the coast and tablelands on infertile soils, often in exposed topographic positions.
Alpine complex	Mosaics of herbfields, grasslands and shrublands. Includes Ericaceae, Asteraceae, Gentianaceae, Ranunculaceae, Poaceae and Cyperaceae. High, snow-prone parts of the southern ranges.
Freshwater wetlands	Wet shrublands or sedgelands, usually with a dense groundcover of graminoids. Includes Cyperaceae, Restionaceae, Juncaceae, Haloragaceae, Polygonaceae, Ranunculaceae and Myrtaceae. Throughout NSW on peaty, gleyed or periodically inundated soils with impeded drainage.
Forested wetlands	Forests of scleromorphic trees (eucalypts, paperbarks, casuarinas) with sparse shrub strata and continuous groundcover of hydrophilous graminoids and forbs. Includes Myrtaceae, Cyperaceae, Ranunculaceae, Blechnaceae, Poaceae. Floodprone plains and riparian zones principally along the coast and inand rivers.
Saline wetlands	Low forests, shrublands and herbfields of mangroves, succulent shrubs or marine herbs. Includes Verbenaceae, Chenopodiaceae, Juncaceae and Poaceae. Coastal estuaries and saline sites of the western plains.
Semi-arid woodlands (grassy subformation)	Open woodlands of scleromorphic trees (eucalypts, acacias), with open understories mostly of chenopod shrubs, usually with strong representation of perennial and ephemeral grasses and forbs, including many ephemeral species. Includes Myrtaceae, Fabaceae, Chenopodiaceae, Asteraceae, Poaceae and Polygonaceae. Low-moderate rainfall regions of the near western plains on clay soils, including infrequently flood-prone sites.
Semi-arid woodlands (shrubby subformation)	Open woodlands of scleromorphic trees (eucalypts, acacias, casuarinas), with open understories of xeromorphic shrubs, grasses and forbs, including many ephemeral species. Includes Myrtaceae, Cupressaceae, Fabaceae, Myoporaceae, Sapindaceae, Asteraceae, Poaceae and Acanthaceae. Low-moderate rainfall regions of the near western plains, including infrequently flood-prone sites.
Arid shrublands (chenopod subformation)	Open shrublands of chenopod shrubs, with perennial tussock grasses and ephemeral herbs and grasses. Includes Chenopodiaceae, Asteraceae, Aizoaceae, Fabaceae and Poaceae. Low rainfall regions of the far western plains.
Arid shrublands (acacia subformation)	Open shrublands of xeromorphic shrubs, hummock or tussock grasses and ephemeral herbs and grasses. Includes Fabaceae, Proteaeceae, Myoporaceae, Asteraceae, Casuarinaceae and Poaceae. Sandy or rocky landscapes in low rainfall regions of the far north-western plains.

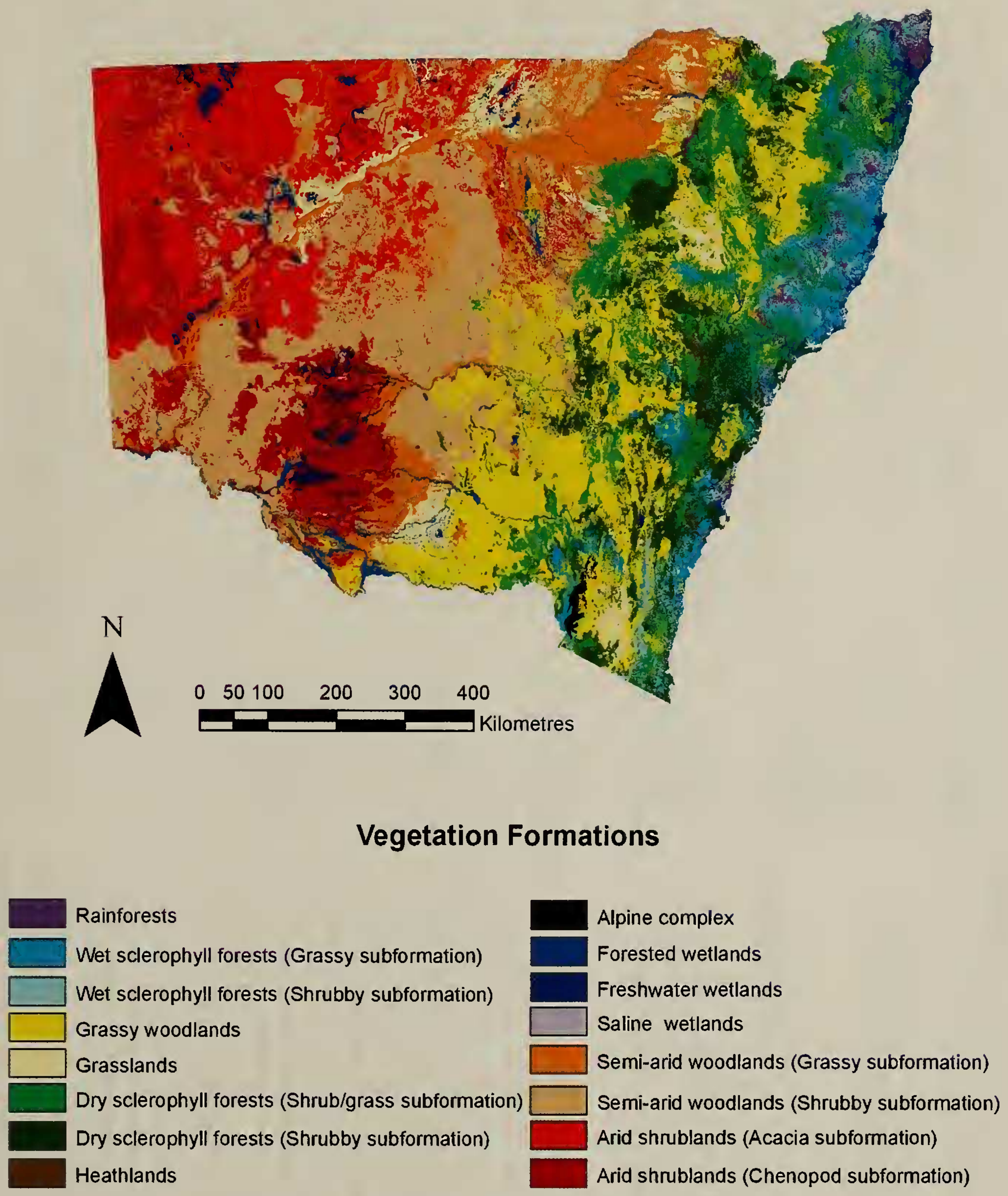

Figure 1. Vegetation map of New South Wales (version 3.0) showing the distribution of 16 formations and subformations (see Table 1 and Keith 2004 for description) prior to intersection with extant mask.

2008). In total, the combined spatial dataset mapped the distribution of 833 geological units across New South Wales and was re-projected to the Australian Geodetic Datum 66 and Lamberts Conformal projection in a geographic information system. As for the vegetation data, the map legend was simplified by assigning each lithological unit to one of 16 substrate types (Table 2). Substrate types were defined on the basis of attributes that were considered important influences on the supply of plant resources: mineral composition; weathering characteristics; texture and depth of derivative soils. The resulting map is shown in Fig. 2.

Table 2. Characteristics of geological substrate types in New South Wales

Substrate type	Origin	Mineral content	Texture	Depth	Examples	Other characteristics
Active floodplain alluvium	Regolith (alluvial)	Fluvial silts, fine sands, muds and clays with high-moderate levels of phosphorus & exchangeable cations	Fine sand & silt, with some clay and localised organic mud. Also includes heavy self-mulching clays	>1m	Coastal & inland floodplains. Richmond River, Moree plains.	Flat-undulating terrain. levees. plains, backswamps and black soil plains. Quarternary deposits
Aeolian (red) sandplains	Regolith (aeolian)	Low-moderate levels of phosphorus and exchangeable cations, calcareous subsoil in SW NSW	Fine sandy loam with clay	>1m	Red sand dunefields and sanplains. Woorinen Formation in Pooncarie district	Flat-undulating terrain, arid & semi-arid climates
Calcarinite*	Sedimentary (marine)	Rich in calcium carbonate	Sandy loams	typically <1m	Very restricted on Lord Howe Island	Flat-undulating terrain, near coast
Estuarine sediments	Regolith (marine/ fluvial)	High concentration of sodium chloride	Silts	typically >1m	Tidal mudflats. Kooragang Island (Hunter River estuary)	Marine & fluvial origin, flat coastal terrain
Felsic intrusives	Igneous	High levels of felsic minerals (quartz, orthoclase & plagioclase) producing soils with high levels of aluminium, potasssium & sodium, but somewhat deficient in phosphorus, magnesium	Coarse-grained weathering to sandy loams	typically >1m, some <1m	Granites, granodiorites, tonalites. New England, Bathurst and Bega batholiths	Steep-undulating terrain, sometimes with tors on hilltops
Felsic volcanics	Igneous	High levels of felsic minerals (quartz, orthoclase & plagioclase) producing soils with high levels of aluminium, potasssium & sodium, but somewhat deficient in phosphorus, magnesium	Fine-grained weathering to loams and clays	typically <1m	Rhyolites, syenites, dacites of the western New England and southern tablelands	Typically steep terrain
High quartz sedimentary	Sedimentary	Abundance of coarse quartz grains bound in a matrix of iron- or aluminium-rich minerals such as siderite or kaolinite with low levels of phosphorus and exchangeable cations, high levels of iron and aluminium	Coarse-grained quartz particles in a fine-grained matrix weathering to sandy loams	typically <1m	Quartzose sandstones.Sydney & Clarence-Morton basins, Pilliga	Steep-flat terrain, limited soil profile development
Lacustrine sediments	Regolith (alluvial)	Moderate levels of most nutrients, depending on source, inundation regime & leaching	Silts & limited sands	typically >1m	Dry or ephemeral lake beds. Mungo Lake, Lake George	Mostly ephemeral lakes of semi-arid zone, some examples in temperate humid tablelands, flat terrain.
Laterite	Regolith (in situ)	High concentrations of iron, aluminium, low concentrations of potassium phosphorus	Loams	<1m	Very restricted in NSW arid zone	Typically on flat terrain, surface or subsurface duricust layer depending on profile weathering
Limestone, dolostone	Sedimentary & metamorphic	Rich in calcite with variable silica component, producing soils with high calcium:magnesium ratios. Also includes domomite, which comprises both calcium and magnesium	Clays and clay loams	typically >1m, some surface exposure	Limestone, dolostone. Jenolan Caves, Bungonia	Steep-flat terrain

Low quartz sedimentary	Sedimentary & metamorphic	Mixture of clay minerals (e.g. montmorillinite, illitie, kaolinite, chlorite) mixed with silt particles of quartz, calcite, etc. producing soils with moderate-high levels of phosporus & exchangeable cations	Clay & loam	mostly >1m	Siltstones, mudstones, shales, greywacke, phyllites, schists. Apsley-Macleay.	Steep-flat terrain
Mafic volcanics & intrusives	Igneous	High levels of mafic minerals (hornblende, pyroxene, olivine, amphibole, biotite) producing soils with relatively high levels of phosphorus, magnesium, iron	Fine-grained weathering to clays and clay loams	typically >1m	Basalt, dolerite, gabbro. Liverpool plains, Geringong volcanics	Often flat-undulating terrain, occasionally steep, the former sometimes producing deep laterised soil profiles
Marine siliceous (white) sandplains	Regolith (marine)	Low-very low in most mineral nutrients, except where influenced by salt spray	Sands	typically 1-5 m	Coastal sand plains. Eurunderee sand mass	Near-coastal, flat sandplains and dunes, often podsolised, mostly marine but some aeolian redeposition (e.g. perched headland dunes)
Residual alluvial clay	Regolith (fluvial)	Low-moderate levels of phosphorus and exchangeable cations	Clay loams	>1m	Riverina plain. Shepparton formation	Flat terrain
Residual alluvial sands	Regolith (alluvial)	Moderate to low levels of most nutrients	Sands & silts	typically >2m	Antecedent stream beds, lunettes, sand plains. Hay plain, rises on the Macquarie-Castlereagh floodplains	Prior streams & inactive alluvial plains, mainly of semi-arid climates on flat terrain
Residual colluvial/ \ alluvial sand & gravel	Regolith (colluvial/ alluvial)	Low-moderate levels of phosphorus and exchangeable cations	Sandy loams & gravels	>1m	Screes, toe slopes. Margins & lower slopes of the Cobar Peneplain	Flat-undulating terrain, Tertiary deposits
Ultramafic igneous & metamorphics	Igneous, metamorphic	Very high levels of mafic minerals and low levels of silica, producing soils with very high magnesium: calcium ratios, high levels of iron, chromium and nickel, and deficiencies in phosphorus and potassium	Fine-grained weathering to clays and clay loams	typically <1m	Serpentinites, peridotites, dunites. Nandewar serpentine belt	Steep-flat terrain, sometimes rocky

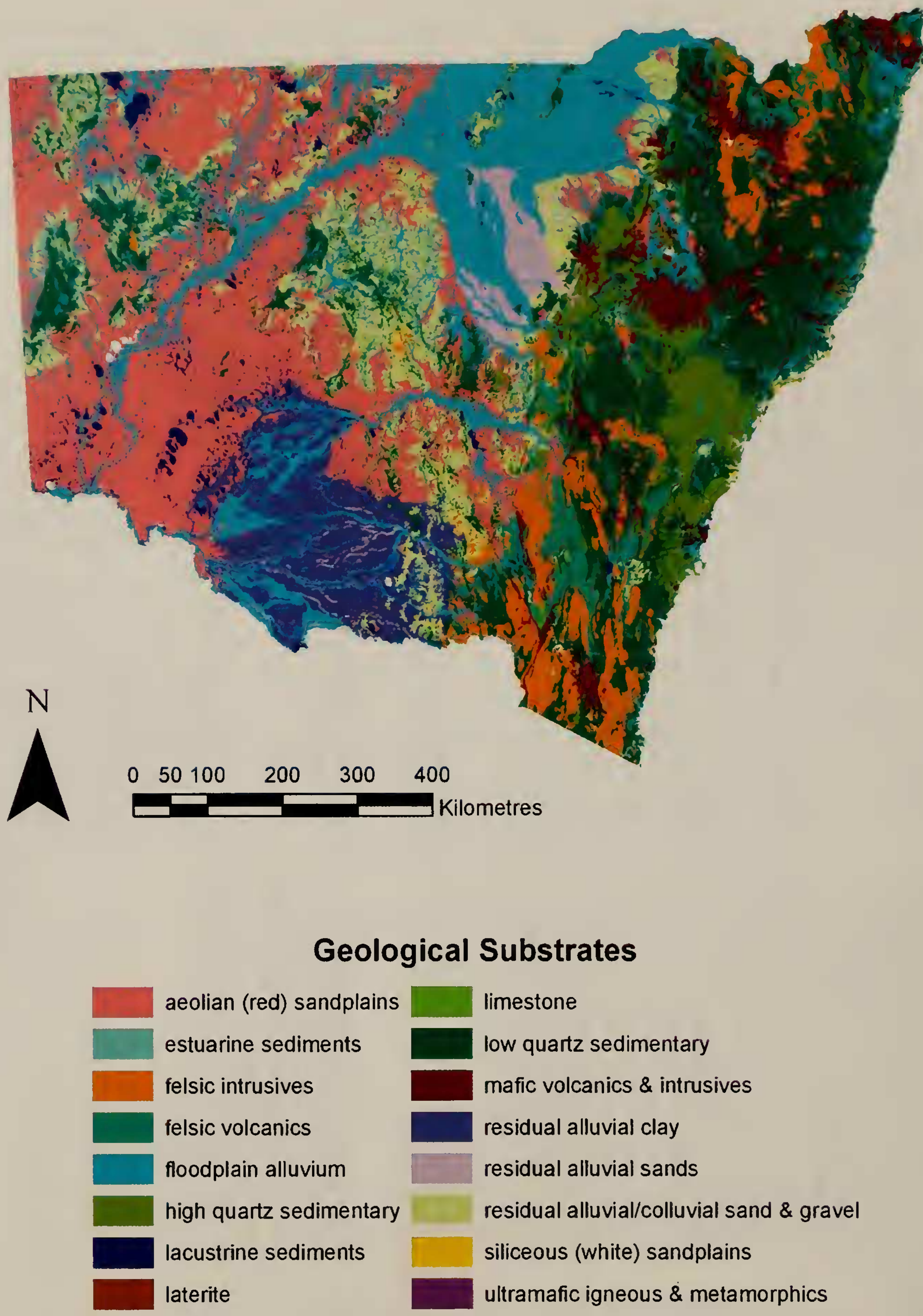

Figure 2. Geological map of New South Wales showing the distribution of 16 substrate types (see Table 2 for description).

Climate surfaces

Spatial grids for monthly precipitation, temperature and radiation parameters were generated by fitting spline functions (Hutchinson 1991) to weather station data across Australia. Using ANUCLIM v6.1 (http://fennerschool.anu.edu.au/publications/software/anuclim.php#overview), the weather station data were aggregated to monthly averages for a 30-year period (1975-2005) and interpolated across the continent on a 9-second latitudinal-longitudinal grid (approx. 250 m). The weekly climate averages were used to calculate the following parameters: MeanTemp- Mean temperature across all weeks of the year; MinTmp- mean of lowest weekly minimum temperature; MaxTmp- mean of highest weekly maximum temperature; DiRngTmp- mean of weekly diurnal temperature ranges; AnnRain- Mean annual rainfall; SummRain – Mean rainfall of December-February; RainDryMth- Mean rainfall of the driest month; MIdry- Mean moisture index of the driest month. Moisture index is calculated from weekly rainfall, evaporation and soil moisture storage (see http://fennerschool.anu.edu.au/publications/software/anuclim/doc/params.html). Spatial data for these parameters were re-projected to the Australian Geodetic Datum 66 and Lamberts Conformal projection in a geographic information system.

Data analyses

To examine the fidelity between vegetation types and geological substrates, 500 randomly located points were generated in a GIS to sample each of the 100 mapped vegetation classes. Subsequently, these were randomly sub-sampled to obtain 1000 points in each of the 16 vegetation formations and subformations. The points sampling vegetation formations and classes were intersected with the geology map (i.e. vegetation cross-tabulated with geology) to estimate their frequencies of occurrence on each substrate type. Similarly, 1000 randomly located points were generated to sample each of the 16 mapped geological substrates, and these were intersected with the vegetation map to estimate the diversity of vegetation formations and classes represented on each substrate type. Calculations of the number of points represented in the cross-tabulations were based on 90th percentile of points to reduce the effect of boundary errors in mapping that may cause spurious occurrences of vegetation types on particular substrates. Thus, the number of substrate types per vegetation unit was taken as the minimum number of substrates accounting for 90% of points within that unit. Pearson correlation coefficients were calculated to assess the association between the area of vegetation classes and formations and the number of substrates that they occupy.

The variation in species composition among vegetation classes attributable to geological substrate and climate was evaluated using ordinations and partial variance analyses (Leps & Smilauer 2003). This required construction of three data matrices characterising the species composition, geological substrates and climatic habitat of vegetation classes. A presence/absence species matrix (99 classes x 1625 species) was constructed from the floristic descriptions (vascular flora) of vegetation classes in Keith (2004), which had been compiled from frequently mentioned species and identified dominant species in the descriptions of source map units. A substrate matrix (99 classes x 16 geological substrates) was constructed from the relative representation of substrates types within each mapped vegetation class, estimated from frequencies of 500 random points per class, as described above. A climate matrix (99 classes x climate variables) was constructed from mean climate parameters across the same samples of 500 random points, which were intersected with each of the nine climate surfaces. Unfortunately, climate surfaces were unavailable for offshore areas, so four vegetation classes (Oceanic Rainforests, Oceanic Cloud Forests, Coastal Headland Heaths and Maritime Grasslands) were omitted from the analysis. Hence the species matrix was reduced to 95 classes x 1500 species.

To determine whether species responses best fitted a linear or unimodal response to environmental gradients, redundancy analysis and canonical correspondence analyses were each carried out on the species matrix constrained by the combined matrices for geological substrates and climate parameters. The first four Eigen vectors of each analysis accounted for a similar proportion of floristic-environmental relationships (25%), although the redundancy analysis accounted for slightly more floristic variation than the canonical correspondence analysis (7.8% cf. 7.2%). A linear response model was therefore assumed for subsequent analyses.

An unconstrained principal components analysis was first carried out on the species matrix. This allowed display of floristic relationships and examination of environmental relationships using indirect gradient analysis to fit vectors representing each variable in the substrate and climate matrices to the floristic ordination.

Two partial redundancy analyses were then carried out to quantify the proportion of floristic variation uniquely attributable substrate types and climatic variables. These were done as constrained ordinations with substrate and climate defined as the environmental and covariable matrices, respectively, and then vice versa for the second analysis (ter Braak & Smilauer 1999). A third partial redundancy analysis was then carried out to determine the combined (union) proportion of floristic variation attributable to either substrate or climate with both sets of variables combined within a single environmental matrix. Finally, the (intersection) proportion of variation attributable to both substrate and climate combined was calculated by subtracting the sums of all canonical eigen values from the first two partial redundancy analyses from the sum of canonical eigen valyes in the third partial redundancy analysis (Leps & Smilauer 2003). All redundancy analyses were carried out in CANOCO for windows v4.02 (ter Braak & Smilauer 1999).

RESULTS

Fidelity of vegetation types to geological substrates

While none of the vegetation formations was restricted to a single geological unit, there was a strong non-random relationship between vegetation formation and geological substrate (χ^2 = 21562, P<<0.001, df = 225). Approximately 27-61% of the extent of each formation occurred on one substrate. More than 90% of the distribution of ten of the 16 formations was restricted to five or less geological substrates and all but one formation was restricted to seven or fewer substrates (Fig. 3). The number of substrates occupied by a vegetation formation was unrelated to the extent of its distribution (R=-0.078, P>0.5, df=15), indicating that vegetation formations were not restricted to a small number of substrates simply by virtue of small distributions. Furthermore, geological substrates supported a limited range of vegetation formations. Four or fewer vegetation formations accounted for more than 90% of the area covered by eleven of the 16 substrate types and none of the substrate types supported more than seven formations. The number of formations per substrate type was unrelated to substrate area (R=0.43, P~0.1, df=15).

At the level of vegetation class, the association with geological substrates was even more strongly expressed. Seven vegetation classes were essentially restricted to a single substrate type, while two-thirds of the 99 classes had at least 90% of their distribution restricted to three or fewer substrates (Fig. 4). As for formations, the number of substrates occupied by a vegetation class was unrelated to the extent of its distribution (R=0.027, P>0.5, df=98).

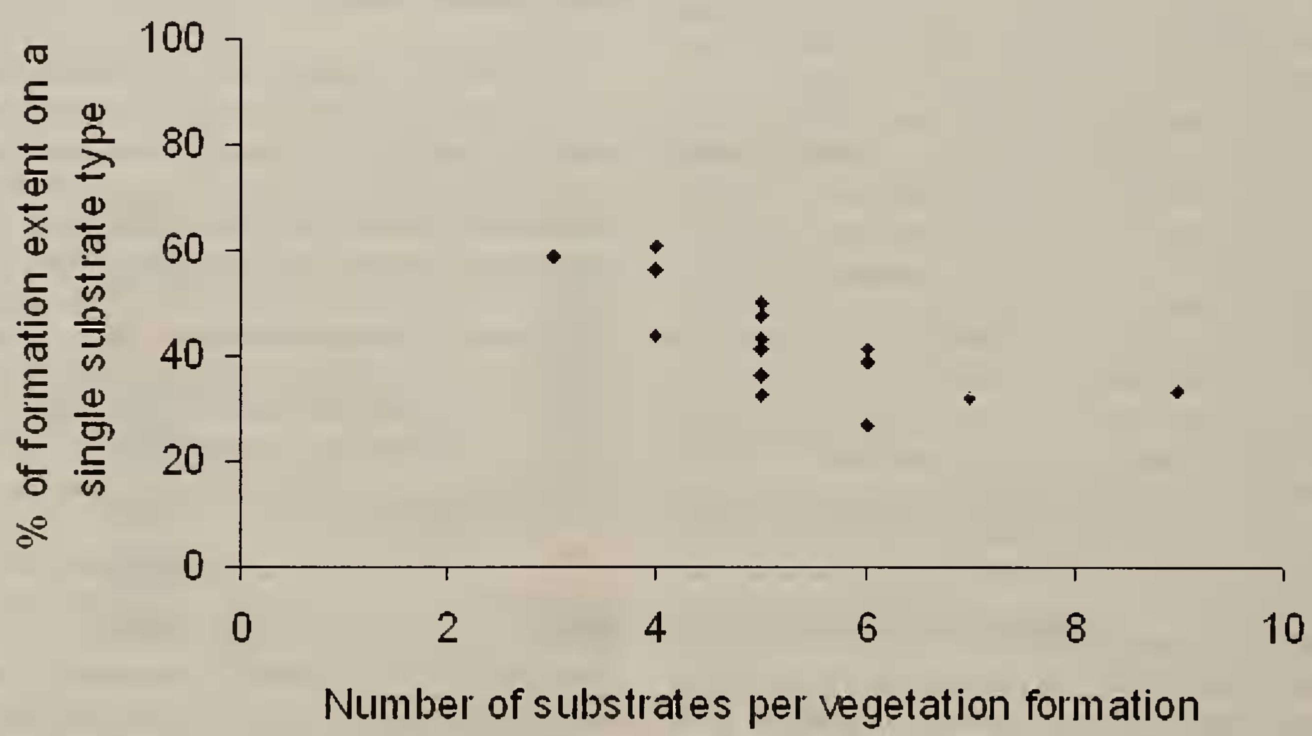

Figure 3. Fidelity of 16 vegetation formations to 16 geological substrate types.

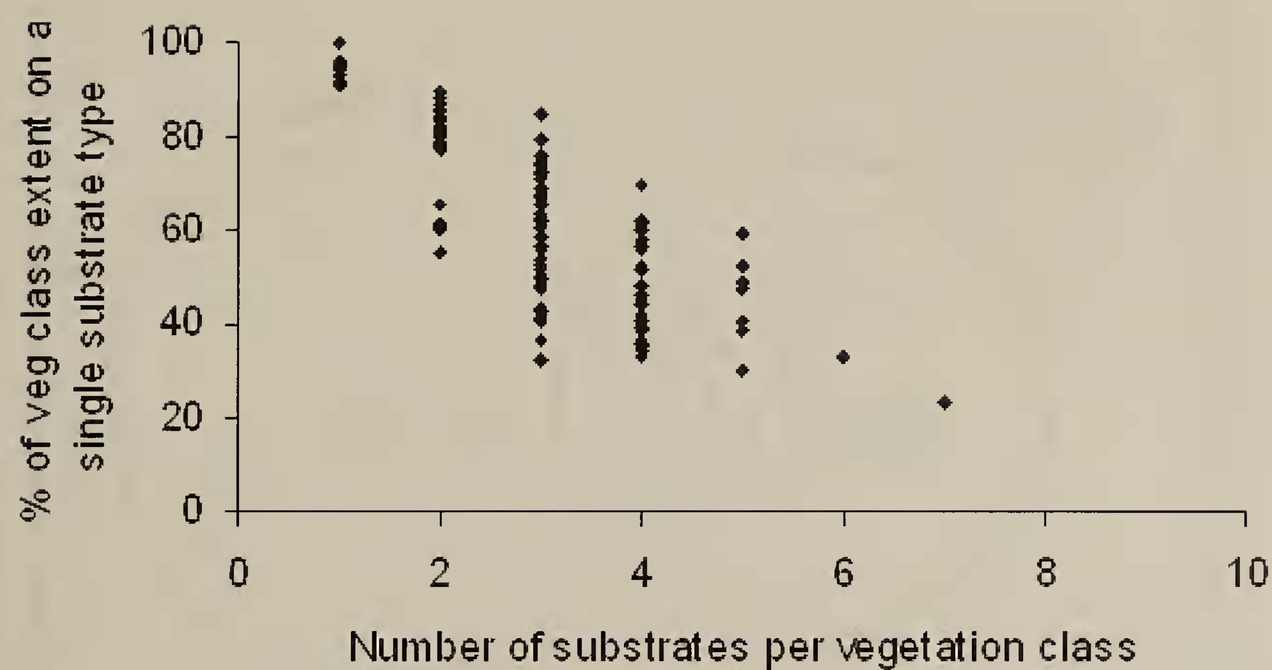

Figure 4. Fidelity of 99 vegetation classes to 16 geological substrates.

Rainforests, both Wet Sclerophyll Forest subformations and Grassy Woodlands were strongly associated with low-quartz sediments and metasediments (Appendix 1). Rainforests also occurred frequently on felsic volcanics, while the wet sclerophyll forests and grassy woodlands were more strongly associated with felsic intrusives. It is likely that the rainforests, grassy woodlands and grasslands were also well represented on mafic volcanics, but much of this substrate has been cleared of its native vegetation. The Heathlands and shrubby subformation of Dry Sclerophyll Forests were strongly associated with high-quartz sediments and siliceous (white) sands of marine origin, but also had significant representation on low-quartz sediments. In contrast, the shrub/grass subformation of Dry Sclerophyll Forests was primarily associated with low-quartz sediments and felsic intrusives (Appendix 1). The Alpine Complex occurred mainly on felsic intrusives and low-quartz sediments. All three wetland formations and the Grasslands were strongly associated with active fluvial alluvium, with lower frequencies of occurrence across a range of other substrates. The shrubby Semi-arid Woodlands and Arid (acacia) Shrublands were strongly associated with aeolian (red) sands, while the grassy Semi-arid Woodlands occurred primarily on floodplain alluvium and residual alluvial clays and Arid (chenopod) Shrublands were on aeolian sands and residual clays (Appendix 1).

The vegetation classes that were essentially restricted (>90% of occurrence) to one substrate type included a range of Rainforests, Dry Sclerophyll Forests, Heathlands and Semi-arid Woodlands (Appendix 2). The geological substrates that supported the broadest ranges of vegetation formations include low- and high-quartz sedimentaries, felsic intrusives and floodplain alluvium (Appendix 1).

Relative influence of geology and climate on vegetation

The Principal Components ordination showed that vegetation classes within the same formation generally clustered together (Fig. 5a). This suggests considerable floristic affinities within formations, even though classes were grouped together within formations on the basis of structural and functional resemblance, rather than compositional resemblance. Indirect gradient analysis showed that geological substrates and climatic parameters account for a diverse array of compositional gradients within vegetation of the region (Fig. 5b). Individual climatic parameters appeared to exert a stronger influence on vegetation, as their vectors were generally longer than those representing individual geological substrates, indicating stronger correlations with species composition. However, geological substrates appeared to exert a more diverse range of influences, as their vectors spanned a greater range of directions than those representing climate parameters (Fig. 5b).

Partial variance analysis showed that, in combination, the full set of geological substrates accounted for a greater proportion of variation in species composition than the climate variables (Fig. 6).

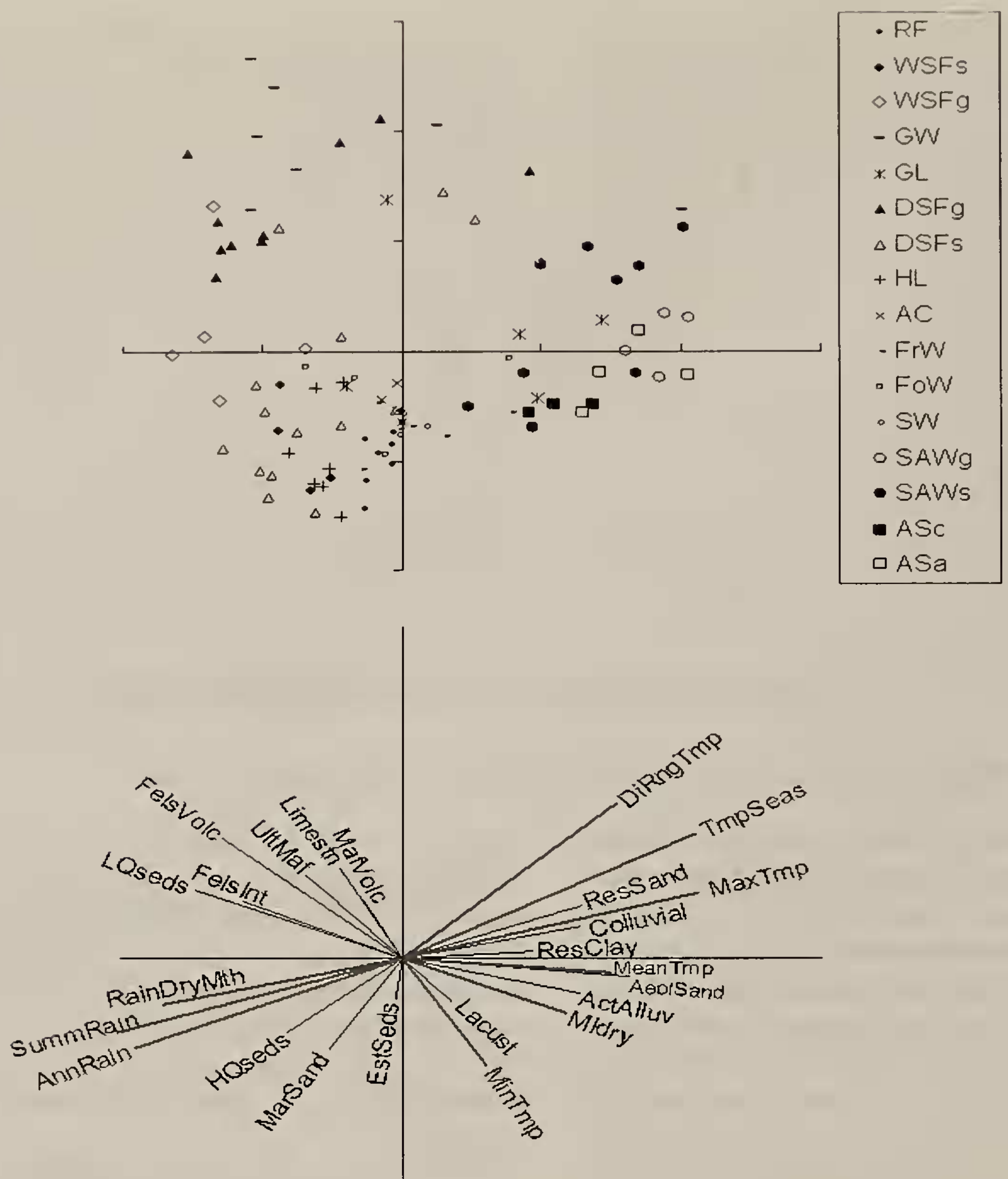

Figure 5. (a) Scatter plot of unconstrained Principal Components Analysis of 99 vegetation classes grouped by formations: RF- Rainforests, WSFs- Wet Sclerophyll Forests (shrubby subformation), WSFg- Wet Sclerophyll Forests (grassy subformation), GW- Grassy Woodlands, GL- Grasslands, DSFg- Dry Sclerophyll Forests (shrub/grass subformation), DSFs- Dry Sclerophyll Forests (shrubby subformation), HL- Heathlands, AC- Alpine Complex, FrW- Freshwater Wetlands, FoW- Forested Wetlands, SL- Saline Wetlands, SAWg- Semi-arid Woodlands (grassy subformation), SAWs- Semi-arid Woodlands (shrubby subformation), Arid Shrublands (chenopod subformation), Arid Shrublands (acacia subformation). (b) Plot of vectors representing 16 geological substrates (thin black lines) and 9 climate parameters (thick grey lines) fitted to the Principal Components ordination. The substrate types are: ResSand- Residual Alluvial Sand, Colluvial- Colluvial/alluvial sand and loam, ResClay- Residual alluvial clay, ActAlluv- Active alluvium, Lacust- Lacustrine sediments, EstSeds- Estuarine sediments, MarSand- Marine sands, Hqseds- High-quartz sedimentary rocks, Lqseds- Low-quartz sedimentary & metamorphic rocks, FelsInt- Felsic intrusives, FelsVolc- Felsic volcanics, UltMaf- Ultramafic volcanic and metamorphic rocks, Limestn- Limestone, MafVolc- Mafic volcanics. The climate parameters are: DiRngTmp- Diurnal range of temperature, MaxTmp- Mean temperature of the warmest month, MeanTemp- Mean annual temperature, MIdry- Mean moisture index (see text) of the driest quarter, MinTmp- Mean temperature of the coldest month, AnnRain- Mean annual rainfall, SummRain – Mean rainfall of December-February, RainDryMth- Mean rainfall of the driest month. Note the vector plot (5b) is enlarged by a factor of 2 relative to the scatter plot (5a).

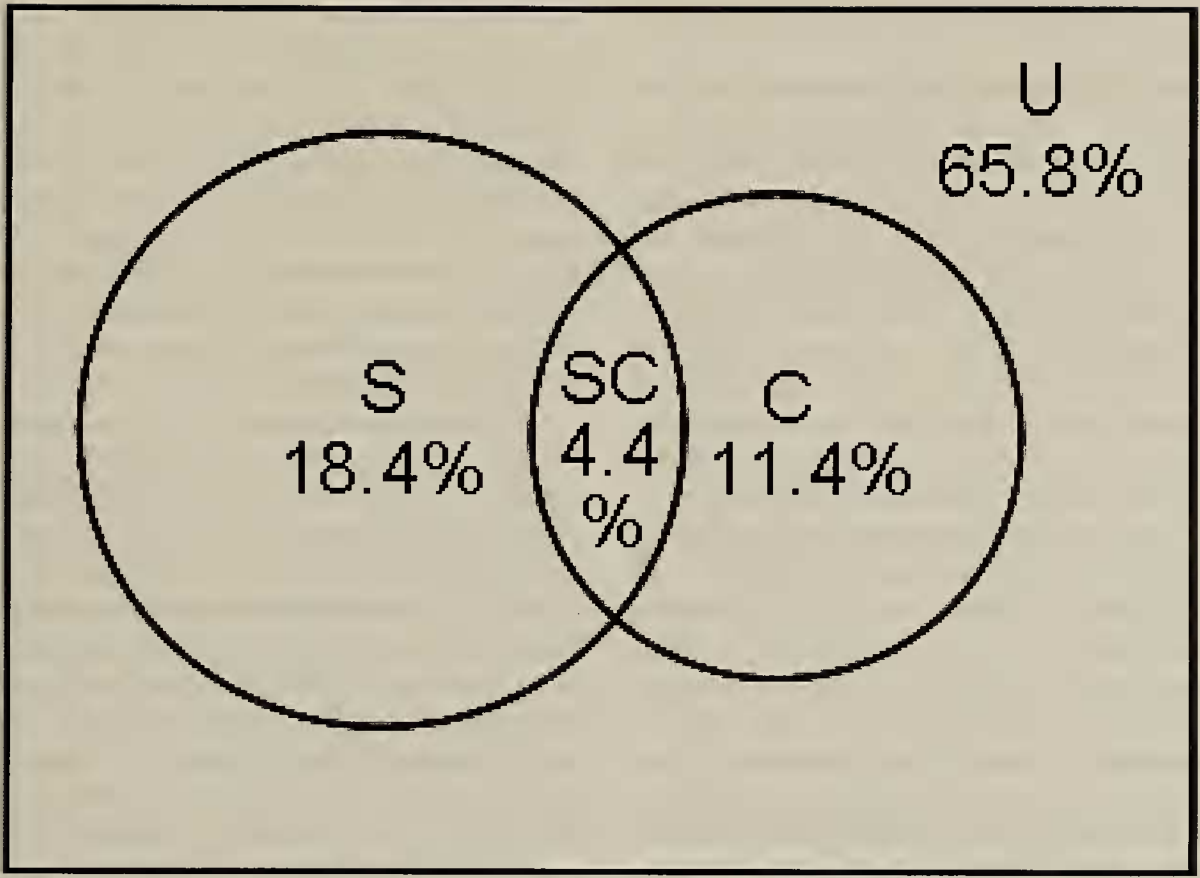

Figure 6. Venn diagram showing portions of variation in floristic composition of vegetation classes attributable to substrate only (S), climate alone (C), both substrate and climate (SC) and unexplained variation (U), as determined by partial redundancy analysis.

Geological substrates and climate accounted for largely independent components of variation in species composition, as only 4.4% of total floristic variation was correlated with both geology and climate in combination. Together, geology, climate and their overlapping component accounted for just over one-third of total floristic variation, leaving two-thirds unexplained (Fig. 6).

DISCUSSION

The influence of geodiversity on vegetation

Vegetation exhibited strong relationships with geodiversity at both class- and formation level across 80 million hectares of south-eastern Australia. Almost one-fifth of floristic variation across this large temperate region was uniquely attributable to geological substrates, independent of climatic variables. Each vegetation formation and class showed strong fidelity to a small range of geological substrates, with some classes restricted to a single substrate type. Stronger fidelity at the class level, relative to vegetation formations, indicates that relationships between vegetation and geodiversity are scale-dependent. At finer levels of vegetation classification than class, a still greater proportion of plant assemblages are restricted to a single type of substrate (e.g. Tozer et al. 2010).

Indirect gradient analysis showed that species composition of vegetation was more strongly correlated with individual climate parameters, notably rainfall, than any single substrate type. However, the compositional trends associated with substrates encompassed a broader array of gradients than those associated with climate parameters. As a consequence, partial variance analysis showed that the substrate types collectively accounted for more variation than a set of parameters encompassing the means and extremes of climatic moisture, temperature and patterns in their seasonality. The overlapping component of floristic variation attributable to both geodiversity and climate was remarkably small.

Among the climate variables, floristic relationships with the three rainfall parameters were positively correlated with one another and negatively correlated with vectors representing maximum temperature, diurnal range and seasonality. This major gradient was associated with the transition from forested vegetation classes to semi-arid woodlands and arid shrublands. Minimum temperature and moisture index of the driest month (which incorporates evapo-transpiration as well as precipitation) displayed somewhat different floristic trends.

A strong contrast was evident between substrates that produce impoverished soils (high-quartz sediments, marine (white) sands) and those that produce more fertile soils (low-quartz sediments, felsic intrusives and volcanics). The former were strongly associated with vegetation types dominated by sclerophyllous shrubs (as understorey or canopy species), while the latter were associated with vegetation types with abundant mesophyllous shrubs and/or grasses. The mafic volcanic substrates generally define the upper limit of this soil fertility gradient, while vectors representing substrates with extreme levels of some mineral elements (ultramafics, limestone) are intermediate between those of mafic and felsic substrates. A similar but more subtle distinction is evident between vegetation classes found within dry-climate regions. Shrubby semi-arid woodlands and arid (acacia) shrublands are associated primarily with impoverished aeolian (red) sands and residual alluvial sands, clays and colluvium, while grassy semi-arid woodlands and arid (chenopod) shrublands are more common on active alluvium and residual clays. Estuarine and lacustrine sediments are uniquely associated with various types of wetlands, which are also associated with active fluvial alluvium.

Support for biogeographic landscape theories

The patterns described above are consistent with early comparative work between the flora of low- and high-quartz substrates in the Sydney region (Beadle 1953, 1966) and with soil-vegetation relationships inferred from early survey work in western New South Wales (Beadle 1948). This work highlighted the association between sclerophylly and soil nutrients, notably phosphorus, which are more abundant in clay minerals derived from mafic substrates than felsic substrates and least abundant in quartz-rich substrates (Table 2).

The observed vegetation-substrate patterns generally support Hopper's (2009) characterisation of two general landscape types: Young Often Disturbed Fertile Landscapes (YODFELs) and Old Climatically Buffered Infertile Landscapes (OCBILs). 'Young' and 'old' in Hopper's sense refer to age of landscape, rather than underlying geology. Hence YODFELs are characterised by relatively fertile soils whose nutrient capital has not been greatly depleted by leaching and which may undergo frequent disturbance related to fluvial or maritime events or mass movement. Their flora is dominated by recently evolved species with long-distance dispersal capabilities, propensity for colonisation, extensive distributions, generalist nutritional and reproductive biology, and tolerance of disturbance (Hopper 2009). The YODFEL profile fits many species of the grassy vegetation formations and subformations, which occur on the more fertile substrates (e.g. low-quartz sediments, volcanics, active alluvium). It also generally fits a large portion of the flora that characterises the three wetland formations, which may generally be viewed as occupying resource-rich sinks within regional landscapes (Keith 2004).

In contrast, OCBILs are characterised by a diversity of ancestral species lineages with limited dispersal and colonisation capability, often with restricted distributions, specialised nutritional and reproductive biology, prominent sclerophylly and limited resilience to physical disturbance. Additional species traits associated with the sclerophyll syndrome were described in mechanistic detail and for a broader range of biota by Orions & Milweski (2007) in their "Nutrient-Poverty/Intense-Fire Theory". The OCBIL profile describes many of the sclerophyll plant species that characterise substrates associated with impoverished soils (e.g. high-quartz sediments, leached marine sands, aeolian sands). Both landscape types appear to extend throughout the humid – arid climatic gradient of the region.

It is noteworthy that much of rainforest flora does not readily fit either profile. Many of the taxa occupy climatically buffered environments and belong to ancient lineages that generally lack recent radiation and have suffered numerous extinctions (Crisp et al. 2004). Yet their habitats are not the most nutrient-impoverished nor very ancient landscapes and many of the taxa are widely dispersed with large distributions, some are ready colonisers.

Axiomatic to both Nutrient-Poverty/Intense-Fire and OCBIL theories is the proposition that plants growing on nutrient-deficient soils with periodically adequate moisture, can synthesize 'excessive' carbohydrates, which are deployed to produce well-defended foliage, large quantities of lignified tissues and readily digestible exudates (Orions & Milewski 2007, Hopper 2009). The nutritional properties of geological substrates therefore define a fundamental basis for evolution of Australian biota and retain a distinctive signature on the present-day distribution of vegetation formations and assemblages in the region of south-eastern Australia examined here. Given their strong influence on contemporary vegetation patterns, geological substrates which, with few exceptions, are essentially fixed landscape features over millenial time scales, appear to impose significant constraints on vegetation response to climate change, especially in landscapes with OCBIL characteristics.

Approximately two-thirds of the floristic variation remained unexplained in the direct gradient analysis. Part of this unexplained variation may include unrepresented influences of soils and climate. For example, substrate types were defined very broadly and often encompass considerable heterogeneity, not only in the complexes of rocks juxtaposed within them, but in the mineral composition and texture and structure of soils produced across catenary sequences of the landscape. The movement and availability of water across the landscape is also an important source of variation that is not fully represented by the climatic variables included in the current analysis. This essential resource almost certainly accounts for some of the unexplained floristic variation, particularly in the wetland component of the biota.

Fire regimes are also likely to account for a fraction of the unexplained variation, as a lack of suitable spatial data precluded any consideration of them in the analysis. Fire regimes have been identified as driving evolutionary forces in Australia and other continents (Bond 2005, Bowman et al. 2009). They are an important component of Nutrient-Poverty/ Intense-Fire theory, as rapid accumulation of nutrient-poor biomass, a result of low rates of herbivory, provides fuel for intense fire, which in turn promotes nutrient poverty through volatilisation (Orions & Milewski 2007). Any remaining variation in floristic composition of south-eastern Australia is mostly attributable to sampling error and inherent spatial autocorrelation, as time lags in vegetation dynamics and limited dispersal processes impose an inherently clustered spatial structure on the composition of biota in the landscape.

Map-based approach to ecological analysis

The map-based approach employed in this study has both strengths and limitations. A major advantage is that it permits a balanced stratified random sampling design across the entire study area. This overcomes a significant constraint for analyses based on field samples over such a large region – the available data are inevitably skewed and non-randomly distributed across the landscape to varying degrees. A complementary analysis based on field samples may nonetheless be profitable, as it permits a more direct location-based exploration of vegetation-environment relationships, and hence exploration of finer-scale patterns than can be represented on sub-continental maps.

A potential limitation of the map-based approach is that imprecision in the boundaries of both maps may have resulted in some combinations of vegetation and substrate types that do not occur in nature, as well as a margin of error in estimated frequencies of association. Non-concurrence of soil, soil parent material and bedrock could occur, for example, where there is significant lateral movement of sediment downslope from its origin. This promotes a tendency for the fidelity of vegetation types to substrate types to be under-estimated (i.e. vegetation types are more restricted to vegetation types than the data indicate). To offset such effects, frequencies in Figs. 3 and 4 were based on the 90th percentile of sampled points, although it is uncertain whether this adjustment adequately compensated spatial errors in the absence of field validation data. A second limitation of the map-based approach is that it does not allow relationships between floristics and environmental data to be explored directly. This was because the species and substrate matrices were based on descriptive data averaged across the mapped range of each unit, rather than location-specific estimates. Thirdly, depending on the methods employed to generate source maps of for corresponding areas, the spatial data for vegetation and geology may not be independent throughout the mapped area. For example, in some cases geological boundaries may have been used as proxies for vegetation mapping and conversely remote sensing of vegetation may have been used to identify geological boundaries. Such non-independence may inflate map-based correlation between vegetation and geology. However, such effects are mitigated by the use of multi-criteria in remote sensing and modelling, only some of which will be non-independent proxies, as well as varying levels of field sampling to directly verify mapped units. Independent reclassification of the vegetation and geological maps further reduced any non-independence. While these methodological issues limited the resolution of relationships that could be examined, the analytical methods employed were sufficiently sensitive to detect major influences of geological substrates on vegetation that, collectively, appeared to be stronger than, and largely independent of climatic influences.

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REFERENCES

Andrews, E.C. (1916). The geological history of the Australian flowering plants. American Journal of Science Series 4 42:171-232.

Beadle, N.C.W. (1948). The vegetation and pastures of western New South Wales. Department of Conservation of New South Wales, Sydney.

Beadle, N.C.W. (1953). The edaphic factor in plant ecology with a special note on soil phosphates. *Ecology* **34**:426–428.

Beadle, N.C.W. (1966). Soil phosphate and its role in moulding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. *Ecology* **47**: 992–1007.

Bowman, D.M.J.S, Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J. (2009). Fire in the Earth System. *Science* **324**: 481-484.

Bond, W.J. (2005). Large parts of the world are brown or black: A different view on the 'Green World' hypothesis. *Journal of Vegetation Science* **16**: 261-266.

Christian, C.S. (1952). Regional land surveys. *Journal of the Australian Institute of Agricultural Science* **18**:140-146.

Crisp, M.D., Cook, L. and Steane, D. (2004). Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philosophical Transactions of the Royal Society London* B **359**:551–1571

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G,J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P. (2009). Phylogenetic biome conservatism on a global scale. *Nature* **458**:754–756

Crocker, R.L. (1944). Soil and vegetation relationships in the lower south-east of South Australia, a study in ecology. *Transactions of the Royal Society of South Australia* **68**:144-172.

Diels, L. (1906). The plant life of Western Australia south of the tropics. Wilhelm Engelmann, Leipzig.

Fraser, L. and Vickery, J.W. (1939). The ecology of the upper Williams River and Barrington Tops districts. III. The eucalypt forests, and general discussion. *Proceedings of the Linnean Society of NSW* **64**: 1-33.

Gray, M. (2004). Geodiversity: Valuing and Conserving Abiotic Nature. John Wiley & Sons Ltd, Chichester.

Hannon, N.J. (1956). The status of nitrogen in the Hawkesbury sandstone soils and their plant communities in the Sydney district:.I. The significance and level of nitrogen. *Proceedings of the Linnean Society of New South Wales*. **81**:199-143.

Hill, R.S., Truswell, E.M., McLoughlin, S. and Dettman, M.E. (1999). The evolution of the Australian flora: fossil evidence. In 'Flora of Australia', vol. 1, second edition. Introduction (ed. A. E. Orchard), pp. 251-320. (CSIRO, Melbourne).

Hopper, S.D. (2009). OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* **322**: 49–86.

Hutchinson, M.F. (1991) The Application of thin plate smoothing splines to continent-wide data assimilation. In Data Assimilation Systems, J.D.Jasper (ed), Bureau of Meteorology Res. Rep. No. 27, Bureau of Meteorology, Melbourne, pp. 104-113.

Johnson, L.A.S. and Briggs, B.G. (1975). On the Proteaceae: the evolution and classification of a southern family. *Botanical Journal of the Linnean Society* **70**: 83–182.

Keeley, J.E. and Rundel, P.W. (2005). Fire and the Miocene expansion of C-4 grasslands. *Ecology Letters* **8**: 693-690.

Keith, D.A. (2004). Ocean shores to desert dunes: the native vegetation of New South Wales and the ACT. NSW Department of Environment and Conservation, Sydney.

Keith, D.A. and Sanders, J.M. (1990). Vegetation of the Eden region, South-eastern Australia: Species composition, diversity and structure. *Journal of Vegetation Science* **1**: 203-232.

Keith, D.A. and Simpson, C.C. (2008). A protocol for assessment and integration of vegetation maps, with an application to spatial data sets from south-eastern Australia. *Austral Ecology* **33**: 761-774.

Lambers, H., Brundett, M.C., Raven, P. A. and Hopper, S.D. (2010). Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil* **334**: 11-31.

Lamont, B. (1982). Mechanisms for enhancing nutrient uptake in plants, with particular reference to mediterranean South Africa and Western Australia. *Botanical Review* **48**:597–689

Leps, J. and Smilauer, P. (2003). Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

McLuckie, J. and Petrie, A.H.K. (1927). An ecological study of the flora of Mount Wilson. Part iv. Habitat factors and plant response. *Proceedings of the Linnean Society of NSW* **52**: 161-184.

Orians G.H. and Milewski A.V. (2007). Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* **82**: 393–423

Pidgeon, I.M. (1937). The ecology of the central coastal area of New South Wales. I. The environment and general features of the vegetation. *Proceedings of the Linnean Society of NSW* **62**: 315-340.

Shane, M. and Lambers, H. (2005). Cluster roots: a curiosity in context. *Plant and Soil* **274**:101–125.

Stewart, A.J., Sweet, I.P., Needham, R.S., Raymond, O.L., Whitaker, A.J., Liu, S.F., Phillips, D., Retter, A.J., Connolly, D.P. and Stewart, G. (2008). Surface geology of Australia 1:1,000,000 scale [Digital Dataset]. Geoscience Australia, Canberra. http:// www.ga.gov,au.

ter Braak, C.J.F. and Smilauer, P. (1999). CANOCO for Windows version 4.02. Centre for Biometry Wageningen, CPRO-DLO, Wageningen, The Netherlands.

Tozer, M.G., Turner, K., Keith, D.A., Tindall, D., Pennay, C., Simpson, C., MacKenzie, B., Beukers P. and Cox, S. (2010). Native vegetation of southeast NSW: a revised classification and map for the coast and eastern tablelands. *Cunninghamia* **11**:359-406.

Troedson, A.L. and Hashimoto, T.R. (2008). Coastal Quaternary geology – north and south coast of New South Wales. Geological Survey of New South Wales Bulletin No. 34. NSW Department of Primary Industries, Sydney.

Webb, L.J. (1954). Aluminium accumulation in the Australian–New Guinea flora. *Australian Journal of Botany* **2**:179-196

Appendix 1. Percentage of 1000 random points in each vegetation formation on each geological substrate type

Substrate type: / Vegetation Formation:	aeolian (red) sands	calcarinite	estuarine sediments	felsic intrusives	felsic volcanics	floodplain alluvium	high quartz sedimentary	lacustrine sediments	limestone	low quartz sedimentary	mafic volcanics & intrusives	residual alluvial clay	residual alluvial sands	residual alluvial/ colluvial sand & gravel	marine siliceous (white) sandplains	ultramafic igneous & metamorphics
Alpine complex	0	0	0	59	3	1	0	0	1	20	16	0	0	0	0	0
Arid shrublands (Acacia subformation)	56	0	0	0	0	14	0	2	0	11	0	0	0	16	0	0
Arid shrublands (Chenopod subformation)	33	0	0	0	0	13	0	5	0	11	0	24	0	14	0	0
Dry sclerophyll forests (Shrub/grass subformation)	5	0	0	22	6	2	10	0	0	47	3	0	0	4	0	0
Dry sclerophyll forests (Shrubby subformation)	0	0	0	11	5	5	36	0	0	28	3	0	0	2	9	0
Forested wetlands	1	0	0	6	3	39	5	12	0	21	7	1	0	2	4	0
Freshwater wetlands	9	0	0	11	1	33	11	7	0	8	2	6	0	2	8	0
Grasslands	10	0	0	4	1	32	1	1	0	6	10	19	0	1	15	0
Grassy woodlands	1	0	0	24	7	5	6	0	1	38	12	2	1	2	0	0
Heathlands	0	0	0	10	5	5	27	0	0	24	3	0	0	5	21	0
Rainforests	0	4	0	4	20	2	7	0	0	43	15	0	0	0	4	0
Saline wetlands	14	0	27	0	0	41	6	12	0	5	0	0	0	2	16	0
Semi-arid woodlands (Grassy subformation)	13	0	0	0	0	41	0	1	0	9	2	16	4	14	0	0
Semi-arid woodlands (Shrubby subformation)	50	0	0	1	1	13	1	1	0	13	0	5	5	13	0	0
Wet sclerophyll forests (Grassy subformation)	0	0	0	24	5	1	15	0	0	44	10	0	0	0	0	0
Wet sclerophyll forests (Shrubby subformation)	0	0	0	20	5	1	8	0	0	61	5	0	0	0	0	0

Appendix 2. Percentage of 500 random points in each vegetation class on each geological substrate type (see Keith 2004 for description of classes).

	aeolian (red) sandplains	calcarinite	estuarine sediments	felsic intrusives	felsic volcanics	floodplain alluvium	high quartz sedimentary	lacustrine sediments	laterite	limestone	low quartz sedimentary	mafic volcanics & intrusives	residual alluvial clay	residual alluvial sands	residual alluvial/colluvial sand & gravel	siliceous (white) sandplains	ultramafic igneous & metamorphics
Subtropical Rainforests	0	0	0	5	2	5	2	0	0	0	50	36	0	0	0	0	0
Northern Warm Temperate Rainforests	0	0	0	6	10	0	19	0	0	0	63	2	0	0	0	0	0
Cool Temperate Rainforests	0	0	0	9	1	0	0	0	0	0	56	33	0	0	0	0	0
Dry Rainforests	0	0	0	4	7	0	8	0	0	0	76	4	0	0	0	0	0
Littoral Rainforests	0	0	0	0	1	11	24	0	0	0	21	4	0	0	1	37	0
North Coast Wet Sclerophyll Forests	0	0	0	4	3	2	22	0	0	0	64	5	0	0	0	0	0
South Coast Wet Sclerophyll Forests	0	0	0	13	5	2	8	0	0	0	71	0	0	0	1	0	0
Northern Escarpment Wet Sclerophyll Forests	0	0	0	9	9	0	0	0	0	0	68	14	0	0	0	0	0
Southern Escarpment Wet Sclerophyll Forests	0	0	0	56	3	0	1	0	0	0	39	1	0	0	0	0	0
Northern Tableland Wet Sclerophyll Forests	0	0	0	16	5	0	1	0	0	0	53	25	0	0	0	0	0
Southern Tableland Wet Sclerophyll Forests	0	0	0	33	12	0	17	0	0	0	30	7	0	0	0	0	0
Sydney Coastal Dry Sclerophyll Forests	0	0	0	0	0	1	89	0	0	0	10	0	0	0	0	0	0
Sydney Hinterland Dry Sclerophyll Forests	0	0	0	0	0	0	93	0	0	0	7	0	0	0	0	0	0
Sydney Montane Dry Sclerophyll Forests	0	0	0	0	0	0	77	0	0	0	22	1	0	0	0	0	0
Coastal Dune Dry Sclerophyll Forests	0	0	0	0	1	9	4	0	0	0	7	0	0	0	0	79	0
North Coast Dry Sclerophyll Forests	0	0	0	1	1	5	60	0	0	0	31	2	0	0	0	0	1
Northern Hinterland Wet Sclerophyll Forests	0	0	0	3	2	4	16	0	0	0	67	6	0	0	0	1	0
South Coast Sands Dry Sclerophyll Forests	0	0	0	0	1	12	9	0	0	0	9	1	0	0	9	59	0
Southern Lowland Wet Sclerophyll Forests	0	0	0	8	2	3	38	0	0	0	48	1	0	0	1	0	0
Northern Escarpment Dry Sclerophyll Forests	0	0	0	82	7	0	0	0	0	0	9	2	0	0	0	0	0
South East Dry Sclerophyll Forests	0	0	0	17	8	1	10	0	0	0	61	0	0	0	3	0	0
Northern Tableland Dry Sclerophyll Forests	0	0	0	36	21	0	0	0	0	0	36	4	0	0	0	0	2
Southern Tableland Dry Sclerophyll Forests	0	0	0	16	16	0	9	0	0	1	52	3	0	0	3	0	0
Western Slopes Dry Sclerophyll Forests	1	0	0	4	6	6	49	0	0	0	26	6	0	0	1	0	0
Pilliga Outwash Dry Sclerophyll Forests	48	0	0	0	0	9	13	0	0	0	10	2	0	4	15	0	0
Wallum Sand Heaths	0	0	0	0	0	19	4	0	0	0	4	0	0	0	1	71	0
Sydney Coastal Heaths	0	0	0	0	0	2	95	0	0	0	2	0	0	0	0	1	0
Northern Montane Heaths	0	0	0	69	16	0	2	0	0	0	4	9	0	0	0	0	0
Sydney Montane Heaths	0	0	0	0	0	0	82	0	0	0	17	0	0	0	0	0	0

	aeolian (red) sandplains	calcarinite	estuarine sediments	felsic intrusives	felsic volcanics	floodplain alluvium	high quartz sedimentary	lacustrine sediments	laterite	limestone	low quartz sedimentary	mafic volcanics & intrusives	residual alluvial clay	residual alluvial sands	residual alluvial/colluvial sand & gravel	siliceous (white) sandplains	ultramafic igneous & metamorphics
Southern Montane Heaths	0	0	0	6	11	0	0	0	0	0	74	5	0	0	3	0	0
Alpine Heaths	0	0	0	72	1	0	0	0	0	0	10	18	0	0	0	0	0
Tableland Clay Grassy Woodlands	0	0	0	41	8	1	1	0	0	0	36	13	0	0	0	0	0
New England Grassy Woodlands	0	0	0	19	12	2	1	0	0	0	48	17	0	0	0	0	0
Western Slopes Grassy Woodlands	1	0	0	5	2	5	9	0	0	0	41	34	0	0	2	0	0
Western Peneplain Woodlands	28	0	0	0	1	18	0	0	0	0	14	0	0	6	33	0	0
Subalpine Woodlands	0	0	0	45	11	0	0	0	0	2	29	12	0	0	0	0	0
Temperate Montane Grasslands	0	0	0	18	5	18	1	1	0	0	17	39	0	0	1	0	0
Semi-arid Floodplain Grasslands	10	0	0	0	0	84	0	0	0	0	2	0	0	0	5	0	0
Coastal Swamp Forests	0	0	0	0	0	65	6	0	0	0	7	0	0	0	0	21	0
Coastal Floodplain Wetlands	0	0	1	2	0	61	10	0	0	0	23	1	0	0	1	2	0
Eastern Riverine Forests	2	0	0	11	8	21	14	0	0	0	33	10	0	1	1	0	0
Inland Riverine Forests	4	0	0	1	0	85	0	2	0	0	1	0	4	2	1	0	0
Inland Floodplain Woodlands	20	0	0	0	0	53	0	3	0	0	2	0	10	2	9	0	0
Coastal Heath Swamps	0	0	0	3	0	16	43	0	0	0	6	1	0	0	1	31	0
Montane Bogs and Fens	0	0	0	53	8	6	3	0	0	0	18	8	0	0	4	0	0
Coastal Freshwater Lagoons	0	0	0	0	0	79	3	0	0	0	5	1	0	0	2	9	0
Inland Saline Lakes	44	0	0	0	0	8	0	37	0	0	5	0	0	0	5	0	0
Mangrove Swamps	0	0	4	0	0	48	12	0	0	0	5	0	0	0	0	30	0
Riverine Chenopod Shrublands	12	0	0	0	0	16	0	9	0	0	1	0	60	0	2	0	0
Aeolian Chenopod Shrublands	70	0	0	0	0	13	0	6	0	0	3	0	6	0	2	0	0
Dune Mallee Woodlands	95	0	0	0	0	1	0	0	0	0	1	0	0	0	3	0	0
Sand Plain Mallee Woodlands	88	0	0	0	0	0	0	1	0	0	3	0	0	0	8	0	0
Semi-arid Sand Plain Woodlands	87	0	0	0	0	4	0	3	0	0	2	0	1	0	3	0	0
Sydney Sand Flats Dry Sclerophyll Forests	0	0	0	0	0	22	36	0	0	0	26	0	0	0	15	0	0
South Coast Heaths	0	0	0	1	0	5	0	0	0	0	43	0	0	0	30	22	0
Northern Gorge Dry Sclerophyll Forests	0	0	0	16	5	0	2	0	0	0	72	4	0	0	0	0	0
Clarence Dry Sclerophyll Forests	0	0	0	2	5	0	10	0	0	0	81	1	0	0	0	0	1
New England Dry Sclerophyll Forests	0	0	0	75	9	0	0	0	0	0	14	3	0	0	0	0	0

	aeolian (red) sandplains	calcarinite	estuarine sediments	felsic intrusives	felsic volcanics	floodplain alluvium	high quartz sedimentary	lacustrine sediments	laterite	limestone	low quartz sedimentary	mafic volcanics & intrusives	residual alluvial clay	residual alluvial sands	residual alluvial/colluvial sand & gravel	siliceous (white) sandplains	ultramafic igneous & metamorphics
Hunter-Macleay Dry Sclerophyll Forests	0	0	0	0	4	2	31	0	0	0	61	0	0	0	0	1	0
Coastal Headland Heaths	0	0	0	1	0	8	5	0	0	0	17	0	0	0	0	69	0
Saltmarshes	0	0	7	0	0	61	4	0	0	0	5	0	0	0	1	22	0
Coastal Valley Grassy Woodlands	0	0	0	16	1	8	15	0	0	0	56	3	0	0	0	0	1
Montane Lakes	0	0	0	2	0	4	0	65	0	0	0	28	0	0	1	0	0
Southern Warm Temperate Rainforests	0	0	0	14	4	1	7	0	0	0	62	12	0	0	0	0	0
Montane Wet Sclerophyll Forests	0	0	0	62	1	0	0	0	0	1	23	12	0	0	0	0	0
Central Gorge Dry Sclerophyll Forests	0	0	0	4	17	0	21	0	0	0	57	0	0	0	0	0	0
Cumberland Dry Sclerophyll Forests	0	0	0	0	2	2	11	0	0	0	52	0	0	0	34	0	0
Southern Hinterland Dry Sclerophyll Forests	0	0	0	83	1	1	0	0	0	0	15	0	0	0	0	0	0
Southern Wattle Dry Sclerophyll Forests	0	0	0	7	1	1	0	0	0	0	91	0	0	0	0	0	0
Upper Riverina Dry Sclerophyll Forests	0	0	0	31	9	1	3	0	0	0	54	1	0	0	0	0	1
Southern Tableland Grassy Woodlands	1	0	0	30	17	1	6	0	0	1	43	1	0	0	1	0	0
Riverine Sandhill Woodlands	14	0	0	0	0	8	0	2	0	0	14	0	30	23	8	0	0
Inland Rocky Hill Woodlands	6	0	0	6	6	2	4	0	0	0	58	0	0	0	19	0	0
Riverine Plain Woodlands	1	0	0	0	0	14	0	0	0	0	4	1	67	11	2	0	0
Inland Floodplain Shrublands	12	0	0	0	0	42	0	24	0	0	1	0	18	1	2	0	0
Subtropical Semi-arid Woodlands	30	0	0	0	0	7	0	1	0	0	21	0	0	0	41	0	0
Desert Woodlands	92	0	0	0	0	1	0	0	0	0	0	0	0	0	7	0	0
North-west Floodplain Woodlands	16	0	0	0	0	78	0	2	0	0	0	0	0	2	3	0	0
Gibber Chenopod Shrublands	19	0	0	1	0	16	0	0	0	0	28	0	0	0	36	0	0
Stony Desert Mulga Shrublands	32	0	0	1	0	5	0	1	0	0	32	1	0	0	29	0	0
Sand Plain Mulga Shrublands	86	0	0	0	0	5	0	2	0	0	2	0	0	0	5	0	0
Brigalow Clay Plain Woodlands	2	0	0	0	0	30	0	0	0	0	20	9	0	4	34	0	0
North-west Plain Shrublands	52	0	0	0	0	11	0	2	0	0	10	0	0	0	26	0	0
Gibber Transition Shrublands	55	0	0	0	0	38	0	3	0	0	3	0	0	0	2	0	0
Alpine Fjaeldmarks	0	0	0	55	0	0	0	0	0	0	45	0	0	0	0	0	0

	aeolian (red) sandplains	calcarinite	estuarine sediments	felsic intrusives	felsic volcanics	floodplain alluvium	high quartz sedimentary	lacustrine sediments	laterite	limestone	low quartz sedimentary	mafic volcanics & intrusives	residual alluvial clay	residual alluvial sands	residual alluvial/colluvial sand & gravel	siliceous (white) sandplains	ultramafic igneous & metamorphics
Yetman Dry Sclerophyll Forests	1	0	0	6	0	2	59	0	0	0	26	7	0	0	1	0	0
North-west Alluvial Sand Woodlands	0	0	0	0	0	84	0	0	0	0	2	0	0	7	6	0	0
Inland Floodplain Swamps	28	0	0	0	1	39	0	15	0	0	4	0	6	1	6	0	0
Floodplain Transition Woodlands	10	0	0	4	1	23	7	1	0	0	17	2	16	7	12	0	0
Western Slopes Grasslands	33	0	0	0	1	46	1	2	0	0	6	8	0	0	1	0	0
Seagrass Meadows	0	0	1	1	0	51	20	0	0	0	11	1	0	0	1	15	0
North-west Slopes Dry Sclerophyll Woodlands	0	0	0	9	4	3	7	0	0	0	57	18	0	0	1	0	1
Alpine Herbfields	0	0	0	29	11	2	0	0	0	2	21	35	0	0	0	0	0
Alpine Bogs and Fens	0	0	0	80	2	2	0	0	0	0	5	11	0	0	0	0	0
Maritime Grasslands	0	0	0	0	0	5	2	0	0	0	1	3	0	0	0	88	0
Oceanic Rainforests	0	5	0	0	0	25	0	0	0	0	0	70	0	0	0	0	0
Oceanic Cloud Forests	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Western Vine Thickets	0	0	0	0	7	2	8	0	0	0	41	41	0	0	1	0	0
Temperate Swamp Forests	0	0	0	24	11	3	3	0	0	0	52	5	0	0	3	0	0
Riverina Grasslands	1	0	0	0	0	2	0	1	0	0	0	0	96	1	0	0	0
Wadi Woodlands	25	0	0	0	0	39	0	1	0	0	15	0	0	0	20	0	0